

THE DISTRIBUTION AND REPRODUCTION OF THE PLAINS
SPADEFoot TOAD, SCAPHIOPUS BOMBIFRONS,
IN IOWA

A Thesis
Presented to
The School of Graduate Studies
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In Partial Fulfillment
of the Requirements for the Degree
Master of Arts

by
Catherine M. Mabry
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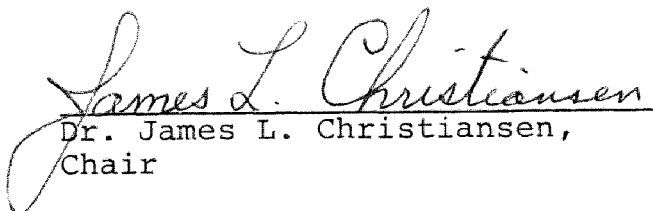
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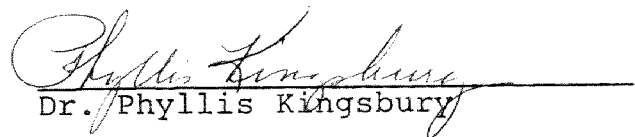
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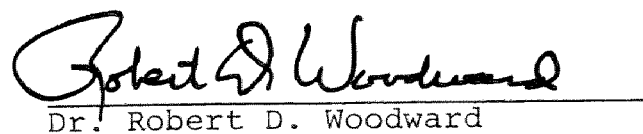
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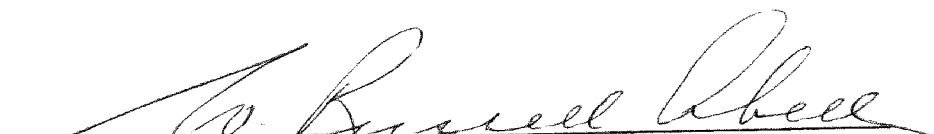
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THE DISTRIBUTION AND REPRODUCTION OF THE PLAINS
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An abstract of a Thesis by
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December 1984
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The problem. The northeastern extreme of the range of Scaphiopus bombifrons occurs in Iowa. This study was designed to determine whether the species should continue to be classified as threatened with extinction in Iowa. At the onset of this study, the species had been found only in a few localities in the loess hills. The study attempted to determine whether or not the species occurred beyond the dry loess soil and adjacent flood plain. Little has been published concerning the reproduction of the plains spadefoot toad. This study attempted to determine time of breeding, number of eggs produced, and the possible relationship among fat, breeding, and above-ground activity.

Procedure. The range was determined by searching for specimens throughout the loess hills on roads during rain or on warm, humid nights. Body length, testes, ovaries and fat bodies were measured to determine size at sexual maturity, cycle of activity and breeding, and gonadal and fat body cycles.

Findings. S. bombifrons was found to occur throughout the loess hills, and no longer merits threatened status. It was not found beyond the deep loess soil. Adult females were more abundant than males, were larger, and attained maturity at a more consistent size. Most individuals were not active below 60°F air temperature, and breeding probably occurred once in a season, usually in June. Mature females produce an average of about 2600 eggs each year. As many as two years were needed for juveniles to attain sexual maturity. Gonads were largest in June, although reproductive capability could apparently be attained through much of spring and summer. Aestivation and hibernation appeared to consume more fat than did the production of gametes.

Conclusions. S. bombifrons is a moderately abundant, possibly recent invader of the loess hills. It appears limited to loess habitats. The species produces a large number of eggs in Iowa, which may help to account for the abundance it seems to have achieved over a period of less than 40 years.

Recommendations. A study of a marked, breeding population should be conducted. It will answer questions concerning life span of individuals, survival over winter, number of breeding periods per year, growth, and could enable estimation of local populations.

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INTRODUCTION

The distribution, habitat associations, and reproductive biology of the plains spadefoot toad, Scaphiopus bombifrons, were studied in Iowa from June, 1982, through September, 1983. Field studies were conducted from June through September in 1982 and 1983 in the loess hills region of western Iowa. The purpose of this study was to determine if threatened status was merited, to identify the precise range of this species in Iowa, and the species' activity and reproductive cycles in the state.

S. bombifrons is one of six North American members of the family Pelobatidae, all of the genus Scaphiopus. Spea bombifrons and Scaphiopus hammondi bombifrons are synonyms of S. bombifrons.

Several studies have dealt with aspects of breeding behavior of S. bombifrons and other species of Scaphiopus. Trowbridge and Trowbridge (1937) studied the cleavage rate of S. bombifrons zygotes and certain reproductive habits of adults in Oklahoma. Bragg and Smith (1942) and Bragg (1944, 1945a) studied breeding and tadpole behavior of S. bombifrons in Oklahoma. Ball (1936) studied the breeding pattern of S. holbrooki in Connecticut. Gosner and Black (1955) studied the effects of temperature and moisture on the breeding cycle of S. holbrooki in New Jersey. Hansen (1958) studied reproductive behavior of S. holbrooki in

Florida. These studies tended to concentrate on the behavioral aspects of Scaphiopus breeding. One purpose of the present study was to provide a more comprehensive picture of reproduction of S. bombifrons in Iowa.

Other studies have dealt with the adaptation of this species to arid conditions. The fossorial habits of species of Scaphiopus are well known. The animals burrow by digging with the hind legs, equipped with wedge-shaped or sickle-shaped spades (Conant 1975). Ruibal et al. (1969) provided a good description of the burrow of S. hammondi in Arizona. Bragg (1944) observed a correlation between burrow depth and soil moisture of S. bombifrons in Oklahoma. Dimmitt and Ruibal (1980) studied S. multiplicatus and S. couchi in Arizona and New Mexico and found that the major stimulus for emergence from burrows was rainfall. Temperature, amount and intensity of rain, amount of rain on the preceding day, time of day, and possibly time of year and soil moisture were also identified as influencing time of emergence. Justus et al. (1977) reported that S. bombifrons in Arizona hatched and developed through metamorphosis in 15 to 19 days. Bragg (1967) stated that S. bombifrons in Oklahoma emerged from a pool as juveniles 14 days after eggs were laid.

The range of S. bombifrons in the United States reflects its aridity-adapted nature. Conant (1975) showed its range as extending from southwestern Manitoba to southern

Alberta, Canada, south through Montana, Wyoming, the Dakotas, Colorado, Nebraska, Kansas, Oklahoma, New Mexico, and northern Texas to Chihuahua, Mexico. It also followed the Missouri River eastward across most of Missouri and occurred in disjunct areas in extreme southern Texas and northeastern Mexico.

Scaphiopus bombifrons may be a recent invader of Iowa. Bailey and Bailey (1941) conducted extensive surveys of anurans in the loess hills. This species was not discovered, however, until 1967 when Huggins (1971) reported specimens from DeSoto Bend National Wildlife Refuge in adjacent parts of Harrison and Pottawattamie counties. Christiansen (1979) added 13 localities from four counties. The present study surveyed the loess area and some adjacent areas to determine the present distribution, and the way it might be influenced by the loess soil.

Scaphiopus bombifrons has been found in habitats ranging from short grass prairies to agricultural land. Bragg (1944) and Conant (1975) described the habitat of S. bombifrons as desert, short grass and mixed grass prairies and open grasslands. Both stated that this species avoided wooded areas and river flood plains. Trowbridge and Trowbridge (1937) studied a population breeding in a temporary pool on agricultural land. The present study determined the habitat associations in Iowa.

The study area. The loess hills are a unique geological feature of western Iowa (Salisbury and Dilamarter 1979). They rise abruptly from the Missouri River flood plain in the west, and gradually decrease in size toward the east. In Iowa the hills extend from Fremont County in the south to Plymouth County in the north, and range in width from three to 20 miles.

Loess is a wind-blown silt that mantles most of Iowa and is the basis of its soil (Salisbury and Dilamarter 1969). Along the western border of Iowa, rather than forming just a mantle, loess was blown from the Missouri River flood plain to form hills up to 200 feet thick. Since then the hills have been eroded to form sharp ridge crests alternating with deep valleys. This landscape is only found elsewhere in China (Prior 1976).

The soil characteristics further contribute to the area's uniqueness, and possibly account for the suitability of the loess hills for aridity-adapted spadefoot toads. Loess soil particles are of small (0.0002 to 0.05 mm), uniform size, creating a porous condition. This allows easy penetration of water, and prevents the soil from holding water. These characteristics, along with sun and wind exposure on the southwestern slopes, create a dry, desert-like environment (Salisbury and Dilamarter 1969).

The arid nature of the loess hills is reflected in their

flora. Little blue stem, side oats grama, big bluestem, lead plant, many-flowered aster and yucca are the dominant plants of the west- and south-facing slopes. On the more mesic north and east slopes, hackberry, elm, sumac, red cedar, black cherry, and ironwood are most abundant (Haglan, Pers. Comm.). More level areas of the loess are planted in corn and soybeans, or are used for pasture. Agricultural crops, primarily corn and soybeans, are the dominant plants of the flood plain.

Several other anurans occur in the study area, although not necessarily in close association with Scaphiopus bombifrons. In order of relative abundance they were found to be: Bufo woodhousei, Bufo cognatus, Rana pipiens, Rana blairi, Rana catesbeiana, Hyla versicolor, Acris crepitans, Pseudacris treseriata, Bufo americanus and Rana clamitans. The preceding data were from field notes and museum records.

Rana catesbeiana, Coluber constrictor, Didelphis marsupialis and Procyon lotor are found throughout the study area and were reported as potential predators of Scaphiopus by Lynch (1964), who also reported several gull species and Heterodon simus as potential predators. Although several gull species pass through Iowa during migration, none were abundant when Scaphiopus was found to be active. H. simus was absent from Iowa, although H. platyrhinos was found there. Crotalus viridis, reported as a Scaphiopus predator

by Stabler (1947), is known from only a few localities in Plymouth County.

Iowa is both wetter and colder than most other areas where S. bombifrons occurs. Average annual precipitation in the central loess hills is about 30.5 inches, and average annual precipitation in the study area ranges from 25.4 inches in the north to 32.2 inches in the south. The greatest rainfall usually occurs in May, June and August (4.40, 4.36 and 4.22 inches respectively), and July is the warmest month with a mean of 76.0°F. Table 1 presents climatological data for March through November (United States Department of Commerce 1982).

MATERIALS AND METHODS

A total of 135 specimens was obtained for laboratory study. Most collecting was done in 1982, but smaller collections from 1978 and 1981 were available from the Drake University research collection, and from field work in 1983. Analysis of data included specimens from all years combined. Collections were made irregularly, usually during or immediately following rains, but also on warm, humid nights.

The most effective method of locating and collecting Scaphiopus involved driving roads at low speeds from approximately one-half hour after sunset until midnight or 0100 h. When a frog was first observed, a flashlight was shined in its eyes and it was then easily collected by hand.

Table 1. Climatological data from Logan, Harrison County, Iowa, from 1951 through 1980 (United States Department of Commerce 1982).

	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.
Mean Maximum*	46.9	63.9	74.8	83.4	87.6	85.3	77.1	66.7	49.0
Mean Minimum*	25.5	38.9	50.4	59.9	64.5	62.2	52.8	41.4	27.9
Mean*	36.2	51.5	62.6	71.7	76.0	73.8	65.0	54.1	38.4
Mean Precipitation**	1.94	3.13	4.40	4.36	3.44	4.22	3.20	2.10	1.21

*Temperatures in °F.

**Precipitation in inches.

Specimens were placed in plastic bags with tags bearing odometer readings at the collection point, then readings were coordinated with journal entries. The specimens were killed by injecting alcohol into the brain and were fixed in 13 percent formalin the morning following collection. They were then tagged with the appropriate data and stored in 6 percent formalin.

All measurements were made to the nearest tenth of one millimeter using vernier callipers. Body size was determined by measuring the snout-urostyle length. The length and width of testes were measured at the widest point.

All specimens were dissected and sexed by gonadal observation. Ovaries were removed and weighed to the nearest 0.0001 gram on a Mettler H54AR balance. Ova of all gravid females were removed and counted under a dissecting microscope.

Fat bodies of both sexes were removed and weighed to the nearest 0.0001 gram. Fat bodies, ovaries and ova were preserved in 13 percent formalin, placed in individual jars, and tagged with the collector's number. After dissection, measurement, and removal of appropriate parts, the specimens were transferred to 6 percent formalin and deposited in the Drake University research collection.

Maturity of females was determined by the presence of enlarged ova, or by the presence of convoluted oviducts in

post-reproductive specimens (Inger and Greenberg 1963). The range of ova sizes was determined by measuring 25 apparently typical ova from the right ovary of nine gravid females using an ocular micrometer mounted on a binocular light microscope, and observed under 40 power magnification.

Sexual maturity of males was indicated by presence of sperm. Sperm smears were made by staining crushed preserved testes with methylene blue. Histological sections of 14 testes taken from males from May through September were prepared to check for different stages of spermatogenesis. Tissues were sectioned at 10 micrometers, stained with Delafield's hematoxylin and eosin, and mounted in clearmount.

Statistical analysis (t-tests and multiple regression) were made on a DEC VAX-11/780 computer at Drake University.

RESULTS

Range in Iowa. In the Iowa study area Scaphiopus bombifrons was found on the Missouri River flood plain and the adjacent loess hills. They were found to breed in these areas and were associated with temporary pools that formed in roadside ditches, at the base of loess bluffs, and in low flooded parts of pastures and fields. It was first reported from Iowa by Huggins (1971). He collected five specimens in and near the DeSoto Bend National Wildlife Refuge adjacent to the Missouri River in extreme northern Pottawattamie and southern Harrison Counties in 1967. At that time five

specimens were also taken east of the Missouri River in Washington County, Nebraska. The next nearest recorded populations were from Butler County, Nebraska, 55 miles southwest of Harrison County, Iowa. This indicated that the Iowa population of Scaphiopus may represent an extension of the range and may not be disjunct.

In 1978 Christiansen (1979) added 13 localities, extending the range through Harrison, Monona, Woodbury and Plymouth counties. Southern Pottawattamie, and all of Mills and Fremont counties were added in 1982 during the course of the present study. Numerous additional localities were found, extending the range throughout the loess hills and the adjacent flood plain (Fig. 1). These localities now represent the northeastern extreme of the range of Scaphiopus bombifrons.

Presence of albinism. On June 14, 1982, an albino female adult S. bombifrons (snout-urostyle length 46.0 mm) was found during a night of very heavy, warm rain. It was taken in Monona County on Highway 12, 4.2 miles south of Rodney, Iowa. The individual was kept alive for over two months with no color change, but was preserved when it appeared to stop eating. It was deposited in the Drake University research collection (CM 44), and lightened slightly after placement in formalin.

The specimen appeared to be a partial albino exhibiting

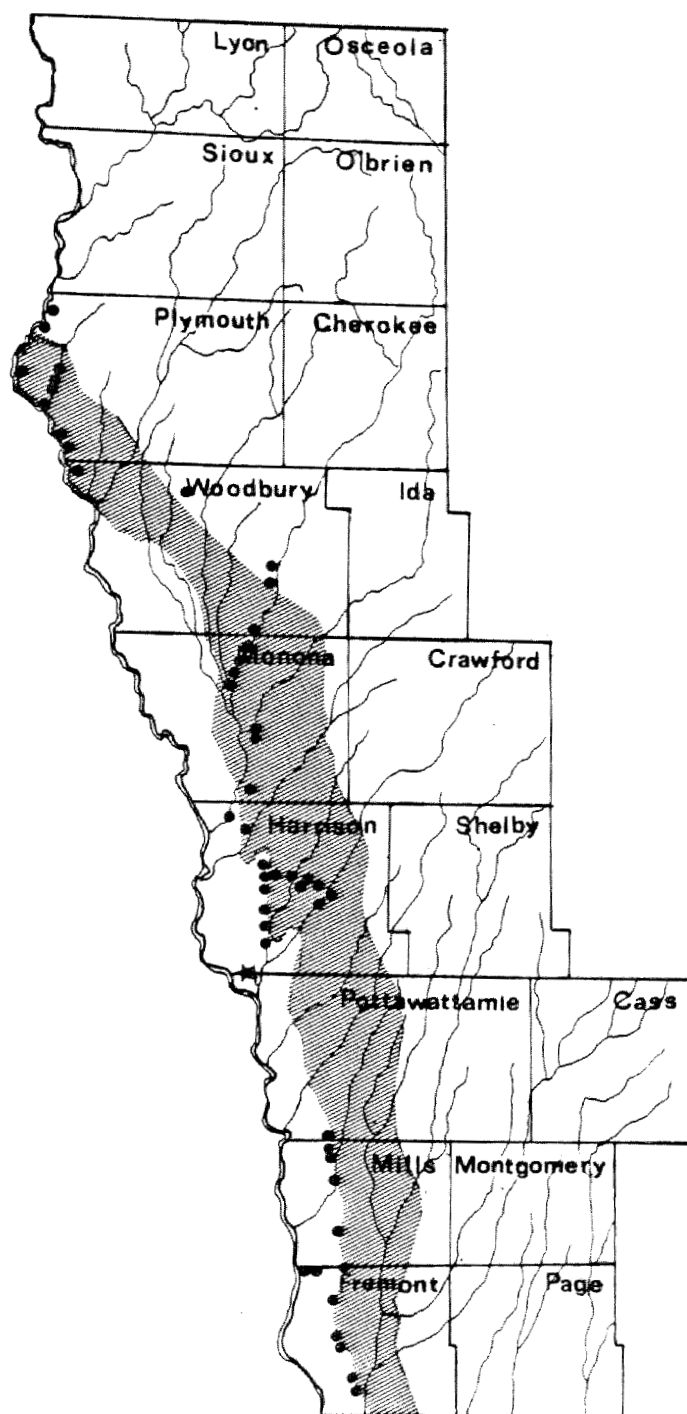


Figure 1. Range of S. bombifrons in Iowa. Boundaries of the loess hills are shown in the shaded area. Star indicates Huggins' (1971) record.

a combination of the different albino categories listed by Dyrkacz (1981). The eyes and internal organs were normally pigmented, leucistic criteria, although the eyes lightened slightly after preservation. The skin was cream to yellowish with brassy flecking corresponding to the normal dorsal pattern of red or yellow spots indicating that xanthophores and iridophores were present. A total leucistic individual would lack all integumentary pigment.

According to Petrovic (1973) and Schwartz (1957), partial albinism (pinto) is caused by local somatic mutation resulting in partial inhibition of melanin deposition. The seven other individuals collected in this area were normally pigmented.

Composition of the population. Of the 135 specimens examined in the study, 62 (45.9%) were female and 73 (54.1%) were male. Sex ratio for adults was 19 (31.7%) female to 41 (68.3%) male. The corresponding figures for juveniles were 43 female (57.3%) to 32 male (42.7%). T-test results showed the sex ratio was significantly different from 50:50 only in adults ($t=.126$, $p=0.01$). Figure 2 shows seasonal changes in percentage of the population that was female for adults and for juveniles. This may have resulted from behaviorally induced sampling error.

Attainment of sexual maturity. The term adult is used here for animals capable of producing gametes. All other

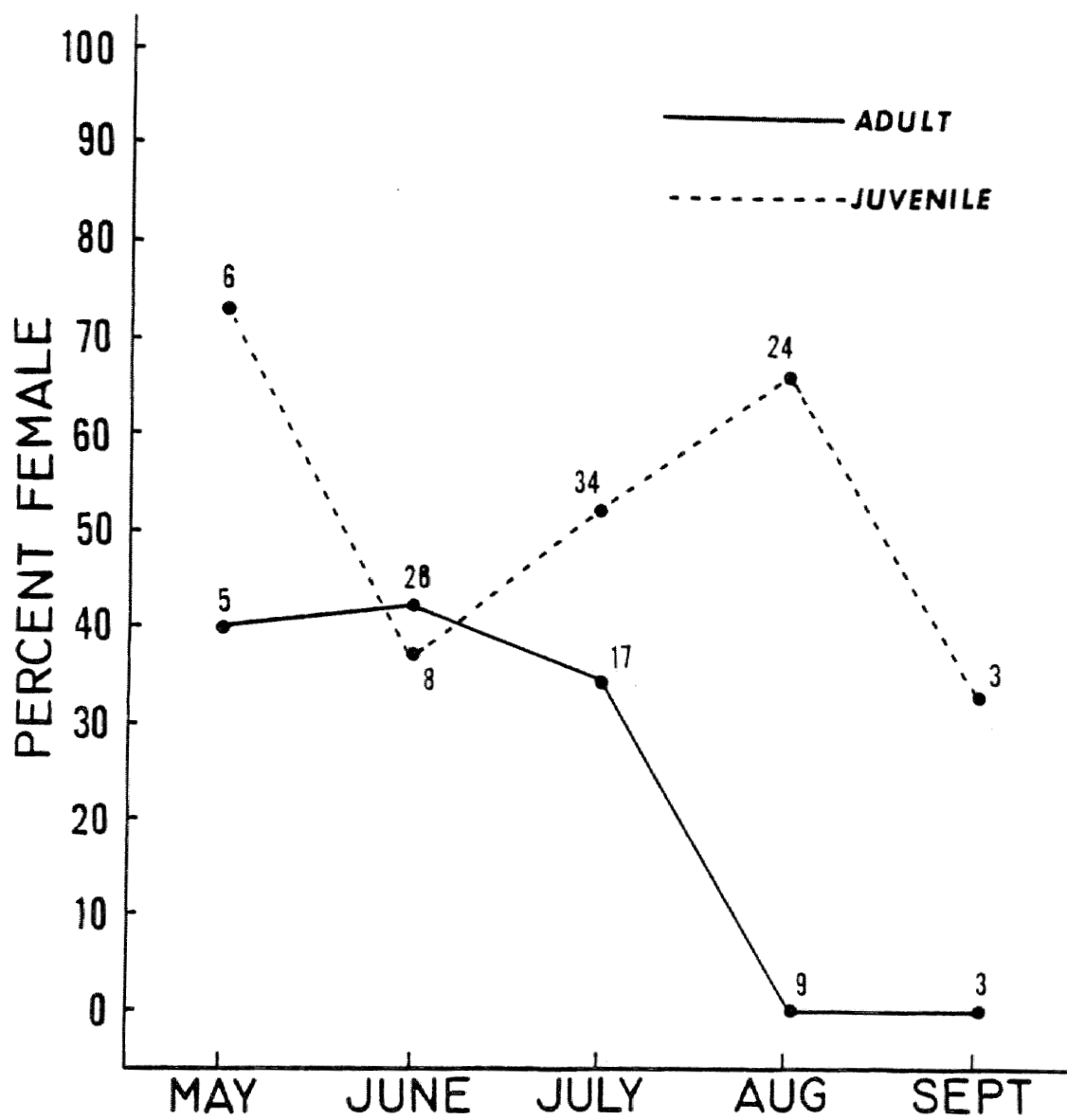


Figure 2. Monthly variation in abundance for female *S. bombifrons* from Iowa, separated into adults and juveniles. Numerals in figure indicate sample sizes.

individuals are referred to as juveniles, varying in size from newly metamorphosed young to individuals of nearly adult size.

Snout-urostyle length was measured for all specimens after preservation. Mean length of all adult females was 49.4 mm (range, 32.5 to 59.6). Mean length of all adult males was 39.3 mm (range, 31.1 to 55.2). The mean for juvenile females was 30.1 mm (range, 19.0 to 40.5). Juvenile males averaged 30.3 mm (range, 21.0 to 38.2). T-test results indicated that the difference in adult male and adult female mean snout-urostyle length was highly significant ($t=5.29$, $P=0.0001$).

The data indicated a wide range at which males became mature. The largest juvenile male was 38.2 mm, but there were 11 adult males smaller than or equal to that size. Similarly, the smallest adult male was 31.1 mm, but 13 juveniles were larger than this. Females appeared to attain sexual maturity at a more consistent size. The largest juvenile female was 40.5 mm. Only one adult female, 32.5 mm, was smaller. Sexual maturity appeared to be more dependent on body size for females than for males.

Cycle of activity and breeding. Favorable air temperatures and rainfall in March and May 1983, failed to initiate emergence of large numbers of Scaphiopus. No individuals were found on 4 March, with the air temperature 53°F and

heavy rain. On 6 May (air temperature 62°F) and again on 18 May (air temperature 54°F), with steady rain on both dates, only nine individuals total were observed, and no breeding choruses were heard.

Breeding of at least some individuals of S. bombifrons in Iowa probably occurred in May, June and July. A gravid female was collected on 18 May 1983, and 25 July 1978. While steady rain was falling on 18 May 1983, no rain occurred on 25 July 1978, although 2.00 inches fell in the collection area several days previously. Air temperature at the time of collection in July was around 68°F. Because a drought occurred in June 1978 (0.88 inch total rainfall), it was unlikely that Scaphiopus bred that month. This may explain the late appearance of a gravid female, and other adult individuals in July that year.

Six gravid females were collected 4-5 June 1981. No rain fell on those dates, although a small amount (0.13 inch) fell in the study area on 3 June. Air temperature at the time of collection could not be determined precisely, but was from 54 to 62°F.

Around 14 June 1982, large numbers of Scaphiopus were thought to breed. Only one gravid female was collected, but several hundred adult specimens were observed during a violent thunderstorm, indicating breeding may have occurred within several days of this. Many adult females were found

that lacked mature ova, indicating that they may have bred shortly before. Air temperature was around 60°F and rainfall amounts in the study area ranged from 1.64 to 3.00 inches. Although favorable breeding conditions again occurred on 30 June and 5 August 1982, only juveniles were found in significant numbers.

The data suggested that S. bombifrons in Iowa did not emerge in large numbers to breed or feed under an air temperature of around 60°F, at least in spring when the soil was cool, and that under normal conditions breeding occurred once in a season, usually in June. This was supported by Fig. 3, which showed steady growth of June emergents through September, with most juveniles reaching maturity the following May. If Scaphiopus bred several times in a single season, this would be reflected the following year by juveniles reaching maturity at different times of season. It may be significant, however, that if favorable conditions do not occur in June, reproductive capability might be maintained for an extended period.

Table 2 compares S. bombifrons' approximate breeding dates in Iowa with dates from other localities. This demonstrated that although S. bombifrons was shown to breed from March to August depending on locality, most breeding was concentrated in May, June and July. The present study implied that mid-June is the primary breeding period in Iowa.

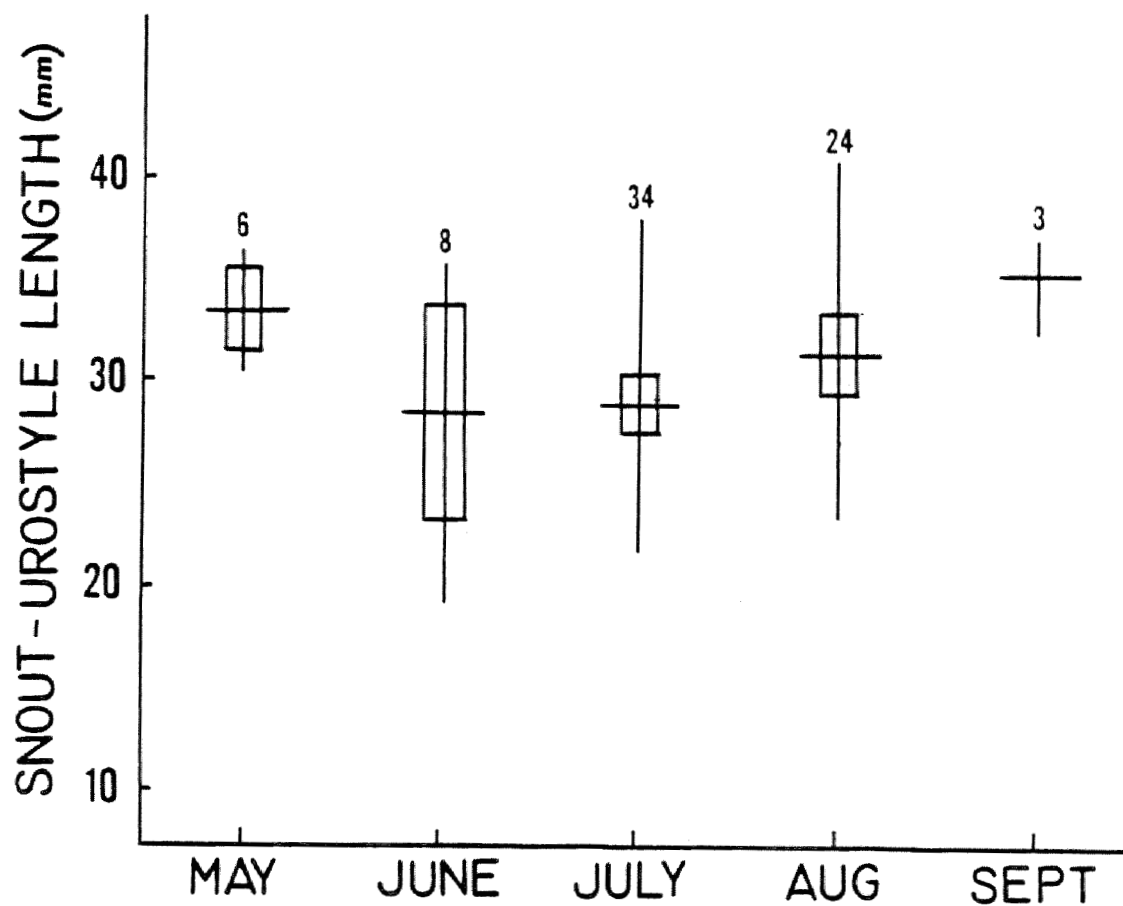


Figure 3. Monthly variation in snout-urostyle length for juvenile *S. bombifrons* from Iowa. Horizontal lines = means; rectangles = 95% confidence limits; vertical lines = ranges; numerals = sample sizes.

Table 2. Scaphiopus bombifrons breeding dates.

Author	Locality	March	April	May	June	July	Aug.
	Iowa			X	X	X	
Mettler et al. (1970)	Missouri				X		
Smith (1934)	Kansas				X		X
Wassersug and Seibert (1975)	Kansas			X			
Black (1974)	Oklahoma			X			
Bragg (1945b)	Oklahoma		X				
Bragg and Smith (1942)	Oklahoma	X		X	X	X	
Trowbridge and Trowbridge (1937)	Oklahoma		X	X			
Gilmore (1924)	Colorado			X	X	X	
Woodward (1982)	New Mexico					X	
Hughes (1963)	Texas				X		
Firschein (1950)	Mexico				X		

Hints as to the timing of maturation of juveniles, and the surface activity of adults were provided by examining the variation of adult snout-urostyle length (Fig. 4). Mean length increased from May to June, remained essentially the same in July, then decreased from July to August and September. The August and September means were nearly equal to the May mean. The data indicated that smaller adults emerged in May with the larger adults not emerging until June. Individuals at the low end of the June range were probably juveniles that hatched early the previous year, and had just reached adulthood, probably in time to breed. The largest individuals dropped out of the sample after July, probably due to death or aestivation, and adult specimens found in August and September were small individuals that probably hatched the previous year, had just matured, and would breed in their third calendar year for the first time.

Timing of metamorphosis, and maturation of juveniles was suggested by comparisons of monthly variation in juvenile snout-urostyle length (Fig. 3). Mean length of juveniles collected declined from May to June. Size then increased steadily from June through September. The data indicated that the May to June decline was possibly due to the addition to the population of newly metamorphosed young, and perhaps to the subtraction from the population of a few of the largest juveniles from the previous year that became mature. The mean size from June to September increased as

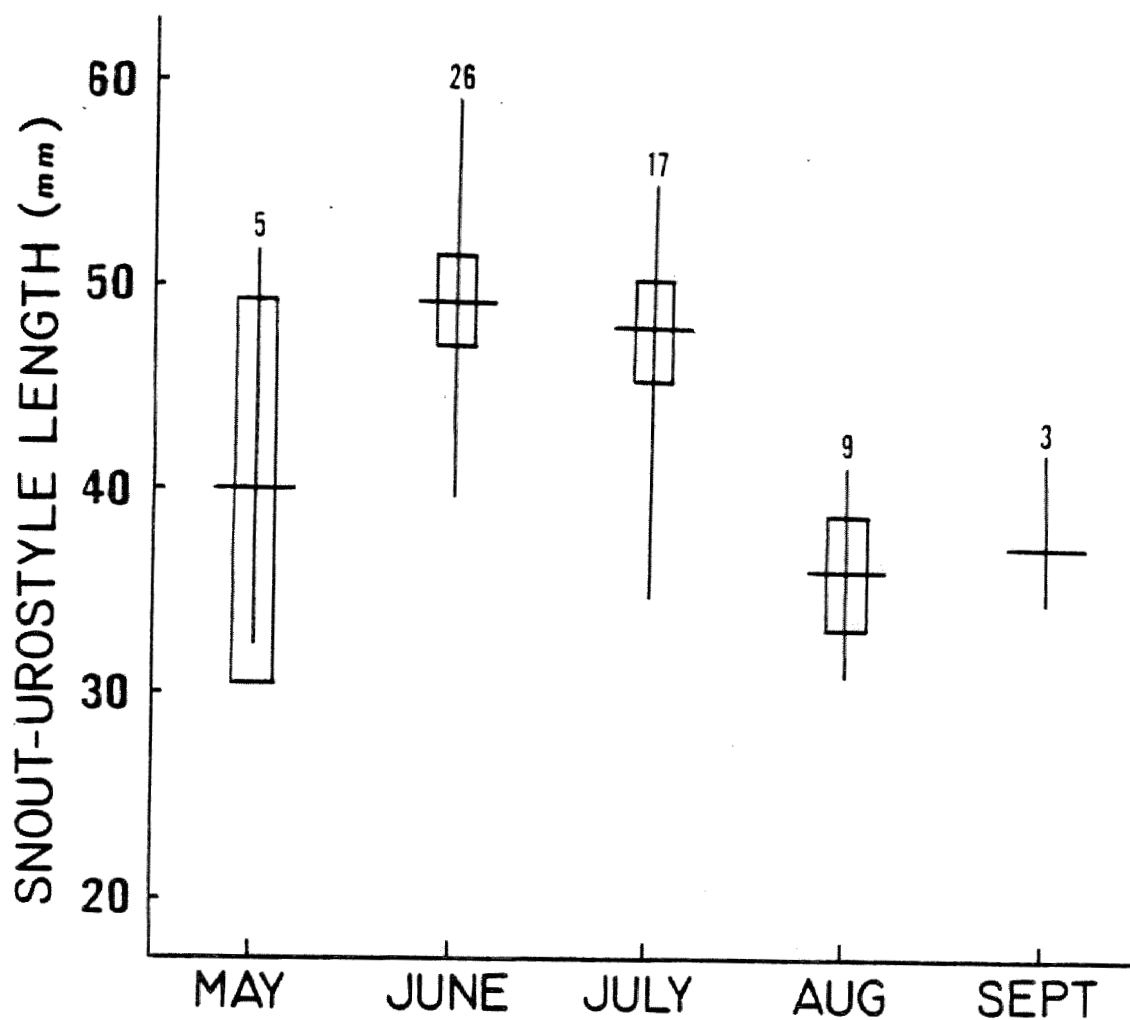


Figure 4. Monthly variation in snout-urostyle length for adult *S. bombifrons* from Iowa. Horizontal lines = means; rectangles = 95% confidence limits; vertical lines = ranges; numerals = sample sizes.

all individuals grew. Individuals from the upper part of the June, July and August ranges were probably late hatchlings or slow growing juveniles from the previous year, and would likely mature the next spring, while juveniles from the low part of the ranges were probably individuals that metamorphosed in June and also would mature the next year. By September juveniles were nearly adult size and would mature early the next year in time to breed.

In summary, most juveniles hatched in June, and probably attained sexual maturity by the following spring in time to breed. Slow growing juveniles or individuals hatched late in the year probably did not mature until late the second year, and did not produce ova until the spring of the third year of life, indicating that one to two years were needed to reach sexual maturity. The appearance in late spring of some very large adults implied that some adults may have persisted in the population for several years.

Figure 5 demonstrates the seasonal variation in numbers of adults and juveniles. Slightly more juveniles than adults were found in May. This could have been from sampling error or a reflection of the ability of juveniles to absorb heat more efficiently and emerge earlier. In June the population was dominated by adults emerging to breed. By July and August the number of adults was dwarfed by the influx of newly metamorphosed juveniles. The data indicated that

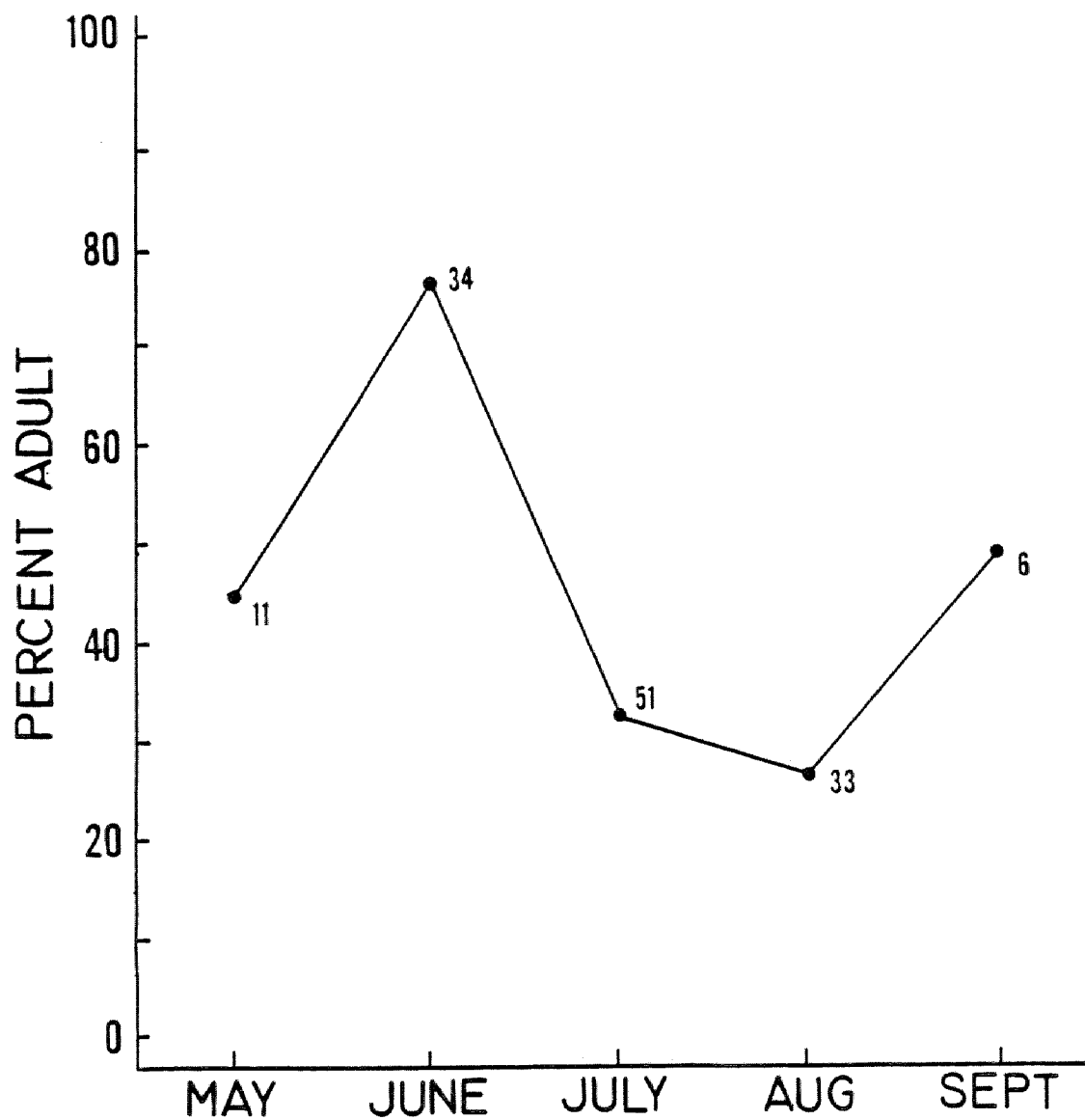


Figure 5. Monthly variation in percentage of abundance for adult *S. bombifrons* from Iowa. Numerals in figure indicate sample sizes.

while juveniles remained active until aestivation in September, most adults in August and September were small and may have represented individuals that just reached maturity.

Gonadal and fat body analysis. A t-test indicated the left and right ovary weights were not significantly different for the 19 adult females examined ($t=.426$, $P=0.9$). The left ovary was chosen for statistical analysis, which showed that ovary weights were highest in June, as would be expected since most females probably bred in June (Fig. 6). Differences in ovary weight were not significant statistically since sample sizes were extremely small, and the samples were heterogeneous, containing pre- and post-breeding females. At least one female with ovaries containing mature ova was found during each of the three months adult females were active during the period of the study. When females with mature ova in the ovaries were excluded, mean ovary weight increased slightly each month.

No females less than 51.6 mm long had mature ova, however, the number of ova was not found to be dependent on length in the small samples available. Total number of mature ova varied from 3844 in a 54.0 mm individual to 1645 in a 55.4 mm individual. Mean number of ova for nine gravid females was 2626. A t-test showed the mean number of ova in the right ovary or to be significantly different from the left ($t=1.09$, $P=0.4$).

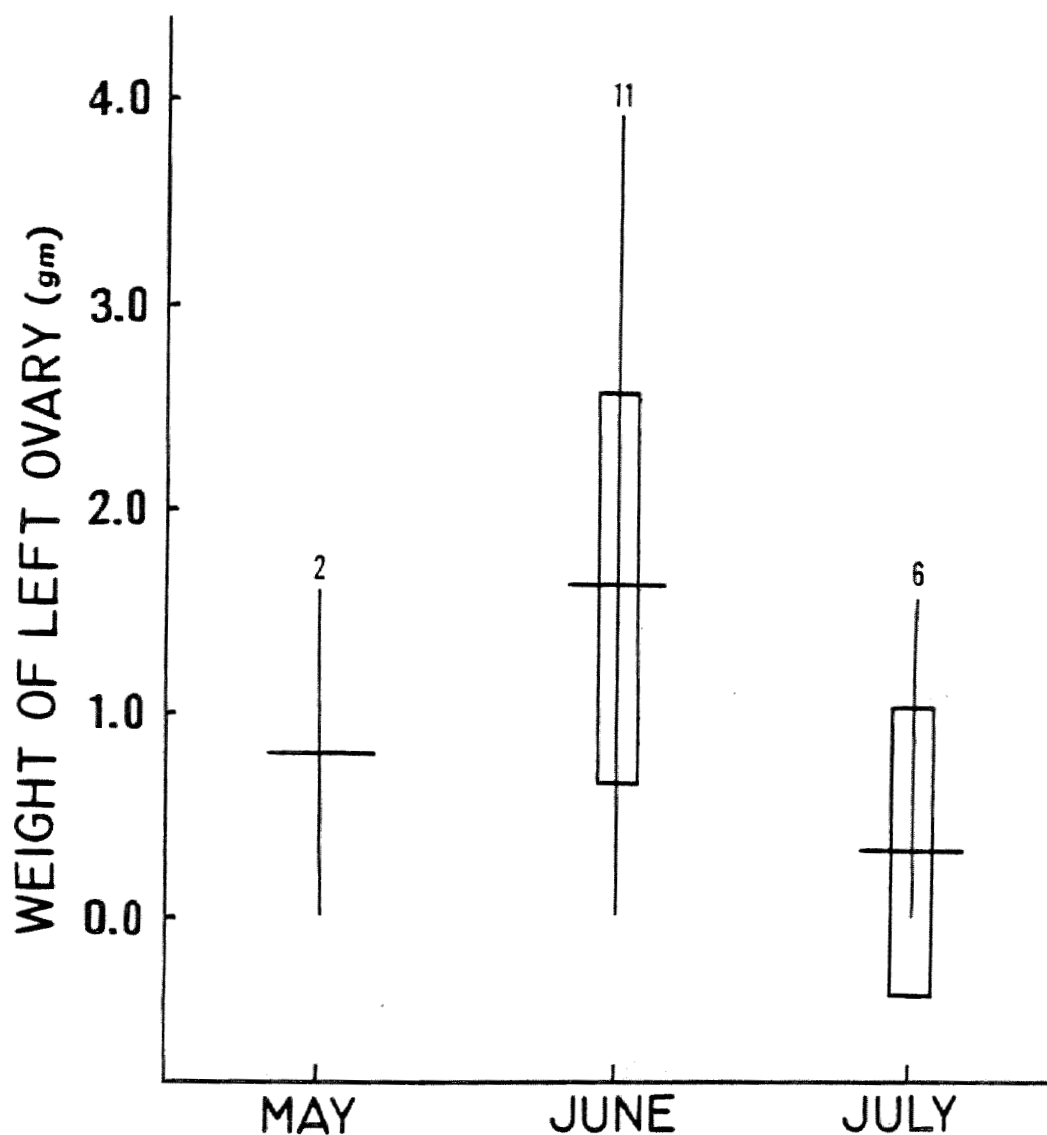


Figure 6. Monthly variation in mean adult females left ovary weight for *S. bombifrons* from Iowa. Horizontal lines = means; rectangles = 95% confidence limits; vertical lines = ranges; numerals = sample sizes.

Mean size of mature ova was 1.29 mm (range, 0.71 to 1.6). Each mature ovary contained a large number of smaller immature ova (lacking pigment), which had a mean size of 0.57 mm (range, 0.38 to 0.9). The immature ova were found in females active in May as well as late July. Immature ova present in May could possibly mature in time for use later in the season if necessary, however, those present in late July were probably saved for the following year.

The length of the left and right testes was not significantly different for the 41 adult males examined ($t=1.09$, $P=0.4$). The left testes was chosen for statistical analysis, which showed that for adult males there appeared to be a seasonal pattern to testes size, with testes length greatest in June when most individuals were probably breeding (Fig. 7). Regression analysis did not show that this was statistically significant, but this might be expected since the trend changed twice during the year, and especially with the small samples involved. Testicular growth might be expected in May and June, with a decline after breeding lasting through August, and with a possible increase in September as a result of the start of testicular growth for the following year. When testes width was used for analysis the results were similar. There was a wide range in the size of testes producing sperm (1.5 to 7.3 mm long).

Histological examination revealed that all stages of spermatogenesis occurred in at least one testes examined

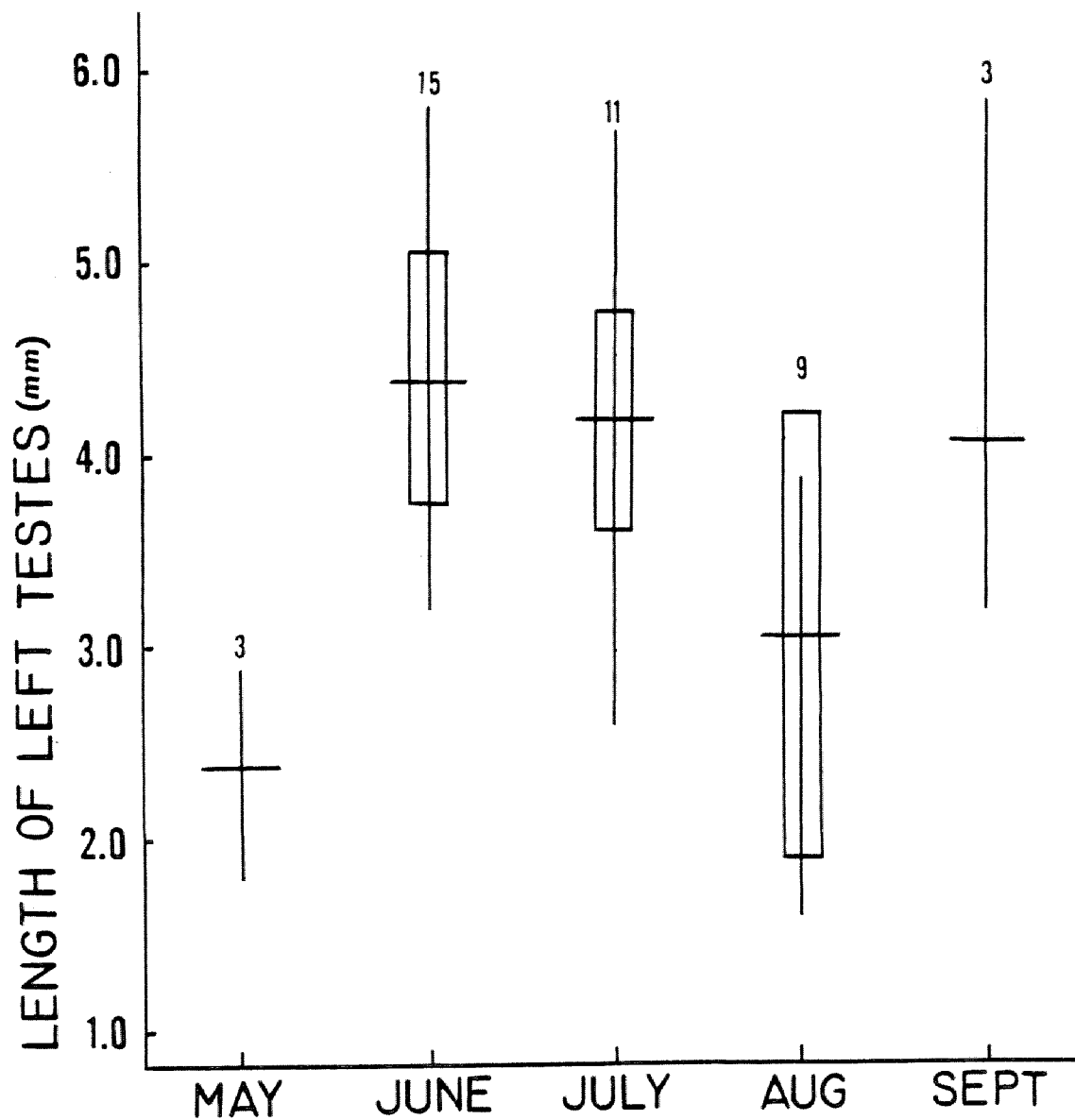


Figure 7. Monthly variation in mean adult male left testes length for S. bombifrons from Iowa. Horizontal lines = means; rectangles = 95% confidence limits; vertical lines = ranges; numerals = sample sizes.

from each month, although they differed in the relative number of spermatogonia, spermatocytes, spermatids and spermatozoa. Spermatozoa were found in the greatest amounts in testes from June.

Mean adult fat body weight for combined males and females was 0.304 gm (range, 0.00 to 1.47). Mean weight was highest in July and lowest in August (Fig. 8). The mean dropped sharply from July to August after most reproduction was completed. However, this may have been a reflection of entry into the population of maturing juveniles in August, and the disappearance of large adults, rather than depletion of fat stores.

Mean juvenile fat body weight was 0.037 gm (range, 0.0003 to 0.408). Mean weight was lowest in May and highest in September (Fig. 9). The mean increased from May to June, fell from June to July, then increased through September as fat was accumulated for hibernation. The June to July decline was probably due to the addition to the population of newly metamorphosed young. Adult and juvenile fat body weights were nearly equal in August and September. Although sample sizes were small, fat body weights for early spring adults were less than those for late fall juveniles, and much less than pre-aestivation July adults. This may imply that summer aestivation of adults, and hibernation of adults and juveniles consumed more fat than did reproduction.

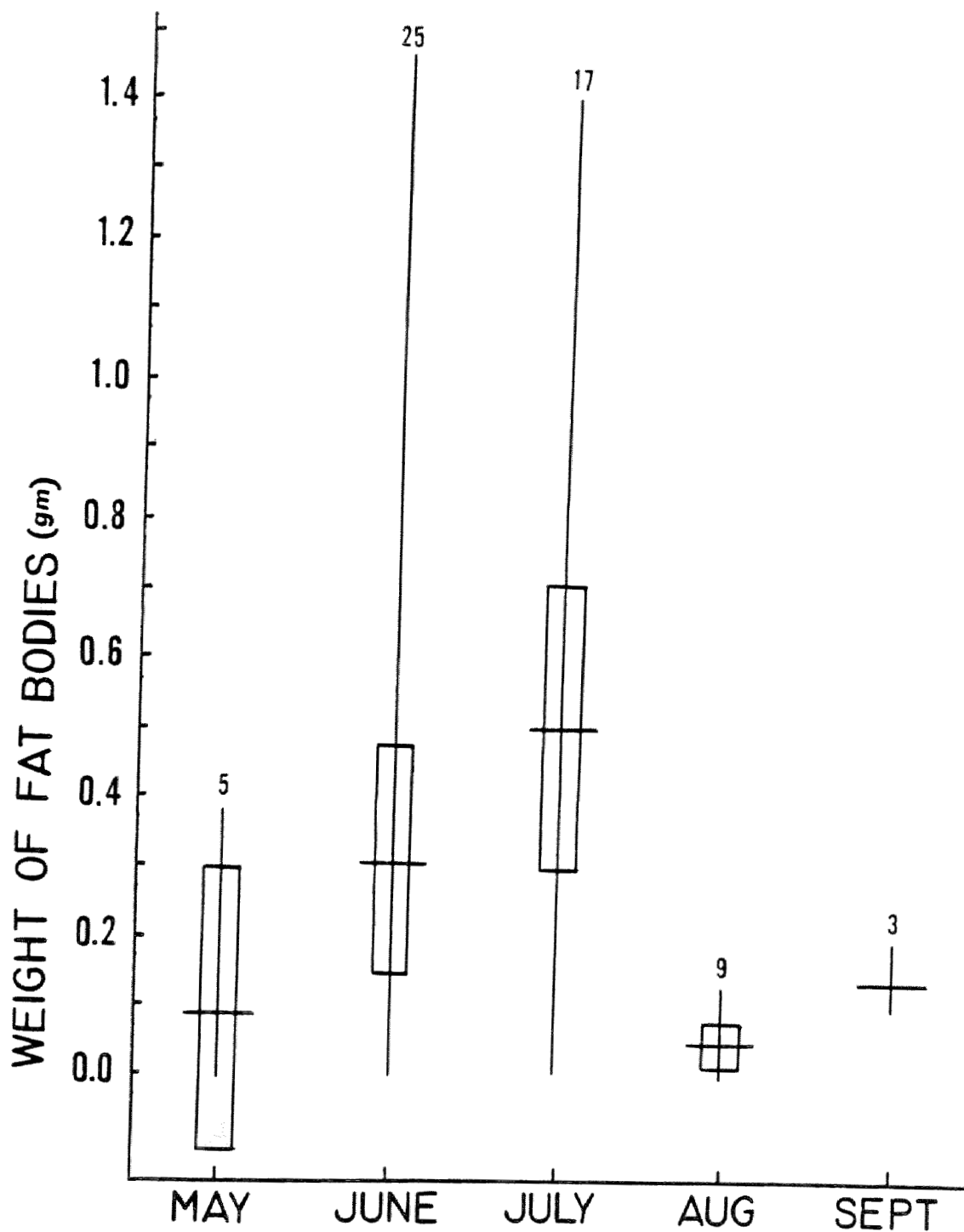


Figure 8. Monthly variation in combined adult male and female fat body weight for *S. bombifrons* from Iowa. Horizontal lines = means; rectangles = 95% confidence limits; vertical lines = ranges; numerals = sample sizes.

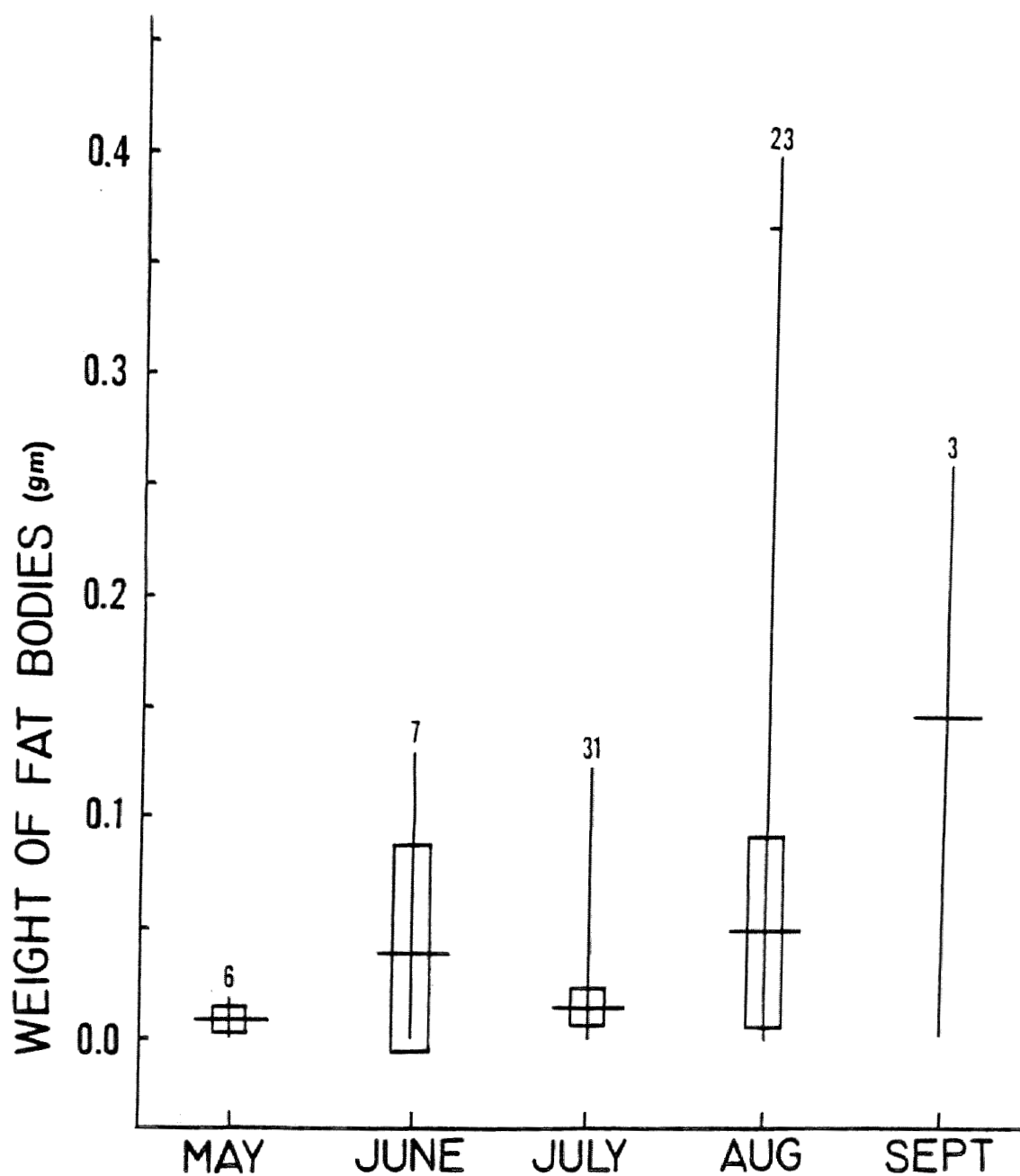


Figure 9. Monthly variation in combined juvenile male and female fat body weight for S. bombifrons from Iowa. Horizontal lines = means; rectangles = 95% confidence limits; vertical lines = ranges; numerals = sample sizes.

DISCUSSION

The range of S. bombifrons in Iowa was shown to extend through the loess hills from Fremont County in the south into Plymouth County in the north, and it was found in numerous localities in this area (see Fig. 1). The extent of the animal's east-west range was less clear. Only two records, both from Woodbury County, have been obtained east of the hilly portion of the loess. Data from Bragg (1944) indicated S. bombifrons could occur further east of the loess. He reported that S. bombifrons was distributed with Bufo cognatus, and stated that the correlation was so close that "we are reasonably sure" in predicting the presence of S. bombifrons in any habitat where B. cognatus occurs. Figure 10 shows the range of B. cognatus, which extended east through the loess hills to the adjacent counties, but not beyond. Because B. cognatus was more abundant and much easier to collect, it could be said with reasonable safety that its range was well-defined and established (see Bailey and Bailey 1941). However, a cold spring in 1983, followed by drought, made collecting east of the hills difficult, and numerous attempts to find Scaphiopus north or east of the present range have thus far failed, indicating that the presence of thick loess may be a requirement for this burrowing species in Iowa.

Scaphiopus may be a recent invader of Iowa or it may have been present since the xerithermal period 4,000 to 7,000

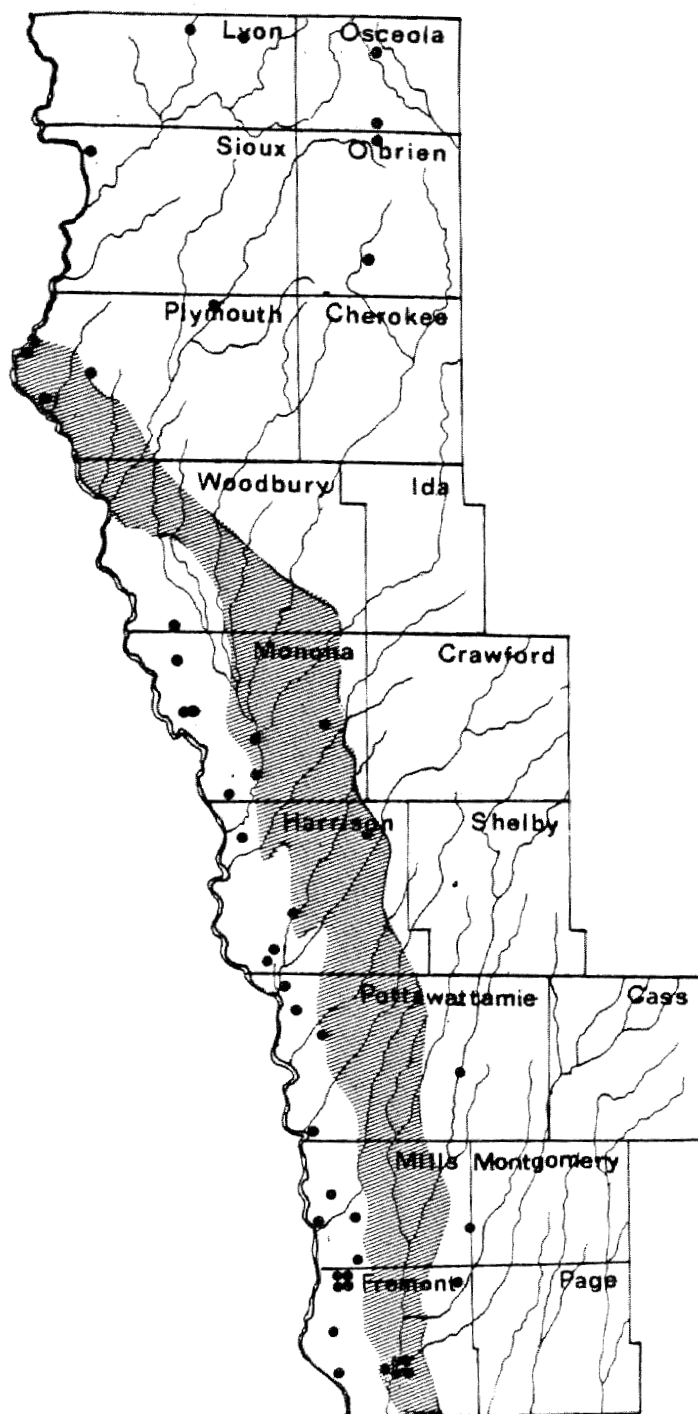


Figure 10. Range of *B. cognatus* in Iowa. Boundaries of the loess hills are shown in the shaded area.

years ago. Evidence suggested that the former is more likely. Extensive collecting was done by Dr. Reeve Bailey (1941) in the loess hills area from 1939 to 1942. His field notes revealed that he collected often during or after warm humid nights when at least some Scaphiopus could be expected to be on the surface. Mettler et al. (1970, p. 780) found a similar situation in Missouri. They wrote of S. bombifrons, B. cognatus and Gastrophryne olivacea, "It might be argued that these three plains species have always been present in central Missouri and collectors had failed to find them. We feel this is unlikely, however, for some of the populations are exceedingly dense and several competent field men . . . have collected in central Missouri in past years." They concluded that S. bombifrons was expanding its range eastward along the Missouri River valley, and was probably dispersing downstream by floods. Further studies are needed to determine the limits of the range of S. bombifrons in Iowa with certainty, and whether the population is expanding.

A partial albino was found in Monona County, Iowa in June 1982, but further searches failed to locate additional albino individuals. The only report of an adult albino that could be found was that of Hughes (1963), who reported two partial albino adult S. bombifrons from Texas. Both specimens had transparent skin except for a few white patches, and a few "extremely small" melanophores on the back. The eyes were normally pigmented. This differed

slightly from the Iowa specimen, which I described as cream to yellowish with brassy flecking caused by a scattering of chromatophores. The only other reports of albinism in Scaphiopus were from tadpoles. Wood (1935) reported albino S. hammondi tadpoles from Utah. Bragg (1957) and Bragg and Black (1970) reported S. bombifrons albino tadpoles from Oklahoma.

Overall sex ratio was 45.9% female to 54.1% male. For adults the figures were 31.7% female to 68.3% male, and for juveniles only, 57.3% were female and 42.7% were male. A t-test determined that the sex ratio was significantly different only for adults ($t=.126$, $P=0.0001$). No other accounts of sex ratios in Scaphiopus could be found in the literature. This difference might be a reflection of behavioral differences between the sexes, possibly resulting from the tendency of males to arrive at breeding pools before females, and to remain there longer.

There appeared to be a strong seasonal difference in activity pattern for adult males and females. Figure 2 showed that there was a higher proportion of males to females in May, June and July. In August and September no adult females were collected. Trowbridge and Trowbridge (1937) observed that adult male S. bombifrons always arrived at the breeding pools first, remained until after the females disappeared, and that more males than females were

evident in breeding congresses. Ball (1936) also reported that males were more numerous in breeding ponds. Such behavioral differences may have resulted in sampling error, and could account for apparent sex ratio differences in adults. In addition, the data may be inadequate to determine sex ratio differences in May and September because sample sizes were small.

Mean body size for adult females was 49.4 mm, and for males 39.3 mm. The data indicated a wide range of body sizes at which males became mature, while females appeared to attain sexual maturity at a more consistent, larger size. T-test results showed that females were significantly larger than males ($t=5.29$, $P=0.0001$). Mean adult body size of Iowa frogs was consistent with the report of Wright and Wright (1949), who stated that mature males were 38 to 52 mm, and mature females were 40 to 57 mm. Firschein (1950), studying S. bombifrons from Mexico, found the size range of males was greater (38.0 to 45.5 mm) than the range for females (39.0 to 43.5 mm). Trowbridge and Trowbridge (1937) reported that adult S. bombifrons from Oklahoma averaged slightly greater than 50 mm, but they did not distinguish between males and females.

There is some disagreement as to whether spadefoots have a predictable reproductive cycle, or are more opportunistic breeders. It has been established (Dimmitt and Ruibal 1980) that rain is the primary stimulus for emergence, with

temperature among the secondary factors in S. couchi and S. multiplicatus. Various authors have noted different minimum temperatures below which breeding does not occur. Hansen (1958) reported that for S. holbrooki in Florida, the lower limiting temperature for breeding was between 45°F and 50°F. Bragg (1945a) reported that S. bombifrons in Oklahoma did not breed below 52°F, but called at 45°F. Trowbridge and Trowbridge (1937) reported 57°F as the minimum temperature for breeding in S. bombifrons in Oklahoma over a three-year period. Gosner and Black (1955) reported no breeding below 9.6°C (49°F) in S. holbrooki from New Jersey.

If the same emergence cues and range of lower limiting temperatures hold true in Iowa favorable breeding conditions could occasionally first occur in March and April, but more often in May, which has a mean minimum of 50.4°F and mean precipitation of 4.40 inches. Favorable temperature and rainfall conditions in March and May, 1983, however, failed to initiate emergence of large numbers of Scaphiopus, possibly because the slow warming of the soil in Iowa would make it likely that the temperature to which the spadefoots are subjected would lag behind the air temperature. The evidence suggested they did not emerge in large numbers below an air temperature of around 60°F.

Around 14 June 1982, large numbers of Scaphiopus were observed, and they were thought to have bred around this time. Favorable conditions again occurred in late June and

early August of that year, but no breeding was evident, and only juveniles were present on roads in large numbers. Although a gravid female and nine adult males were collected in late July, 1978, drought occurred in June of that year possibly postponing breeding, making this the first breeding of the season.

Trowbridge and Trowbridge (1937) also reported that no S. bombifrons appeared after the first breeding, even when proper conditions occurred, and based on their data from Oklahoma, and that of Gilmore (1924) from Colorado, they concluded that S. bombifrons exhibited a well-marked breeding season not exceeding two weeks, with late appearances the exception rather than the rule. They added that geographical location may influence the timing, but not the length of the breeding season.

Conversely, Bragg (1945a), who also studied S. bombifrons in Oklahoma, said spadefoots exhibit what he called a "xeric" breeding pattern, characterized principally by lack of a definite breeding season, and also by breeding in temporary pools, and by breeding only during or immediately following rain. Gosner and Black (1955), in their study of S. holbrooki in New Jersey, also concluded that Scaphiopus had a xeric breeding pattern. They added rapid larval development as a xeric pattern characteristic. The xeric pattern was supported by evidence from Ball (1936), who reported that oviposition occurred twice in a season in

a population of S. holbrooki in Connecticut. He stated that not all the females in a given locality necessarily oviposit at the first favorable opportunity. Hansen (1958), who studied S. holbrooki in Florida, also reported instances of multiple breeding in a single population, and Bragg and Smith (1942) reported three S. bombifrons breeding congresses in a single population in Oklahoma.

Breeding dates of S. bombifrons from around the United States were summarized in Table 2. Although S. bombifrons elsewhere fit the xeric pattern in breeding any time from March to August, most breeding in Iowa occurred in June. It is therefore the opinion of the writer that S. bombifrons in Iowa may have a well-marked breeding season, with a few individuals, probably due to unfavorable conditions, breeding later in the year. This needs to be tested through the study of a marked population over several years.

Hansen (1958) summarized breeding data for S. holbrooki in the eastern United States. His summary showed that in the southern part of the range S. holbrooki was observed to breed in every month of the year except November, with breeding fairly evenly distributed among the months. In the middle latitudes breeding occurred from March to August, with breeding concentrated in March through June. In the northern latitudes breeding occurred from April through August with breeding concentrated in April and May. This suggested a condensing of the breeding activity in the

earlier warm months in more northern latitudes, with an increasing bias toward June. Possibly the extreme of this condition is represented in the Iowa population.

Monthly variation in adult snout-urostyle length was plotted in Figure 4. The largest adults were active earlier in the year, after which they dropped out of the sample. Most adults found in August were probably newly matured individuals, and were small. Monthly variation in juvenile snout-urostyle length was plotted in Figure 3. Except for a small decline from May to June, body size increased as all individuals grew. These patterns indicated that juveniles hatched early in the summer, matured in time to breed the next year, while slow growing individuals and those hatched later probably did not breed until the third year of life. These data are inconsistent with the observations of others. Pearson (1955) found that juvenile S. holbrooki in Florida matured during the second year after metamorphosis. Trowbridge and Trowbridge (1937), based on growth rates in the laboratory, stated that S. bombifrons in Oklahoma would not be expected to reach sexual maturity before the end of the second year. Ball (1936), studying S. holbrooki in Connecticut, found that three years were needed to reach maturity. It remains the opinion of the writer that most juvenile S. bombifrons in Iowa mature in time to breed in their second year, while a few slow growing individuals or late hatchlings do not breed until their third calendar year.

Seasonal differences in emergence pattern for adults and juveniles were found (Fig. 5). Slightly more juveniles were found in May than in June. However, June was dominated by adults emerging to breed. Most adults (all adult females) dropped out of the sample after July, probably due to either death or aestivation. Juveniles regularly emerged on warm, humid nights through September, apparently to forage. Kellogg (1932) also found that young emerged on summer nights independent of rain. However, Bragg (1944) and Ball (1936) reported adults also emerged at night independent of rain to forage.

There appeared to be a slight pattern in the seasonal variation of testes length and ovary weight, with both greatest in June (Figs. 6 and 7). No accounts in the literature could be found where testes size and ovary weight were measured for Scaphiopus of any species, so comparisons with the observations of others could not be made. However, because both ovary weight and testes length were greatest in June, the data tended not to support the conclusions reached by Bragg (1945a) and Gosner and Black (1955) that Scaphiopus have a xeric breeding pattern. However, at least one individual with mature ova, and one with spermatozoa was found during each month of activity, indicating that some individuals may gain reproductive capability at any time during the summer, supporting the xeric pattern to a degree.

Hansen (1958), studying S. holbrooki in Florida, concluded that in the absence of ovulation, females carry a full compliment of mature ova through the year. Males from the same period were found to have viable sperm in the testes throughout the year. He also found that even the most mature ovaries possessed some immature eggs in various stages of development, as did Scaphiopus in Iowa, and suggested that post-mature ova might be replaced by newly developed eggs. For the most part S. bombifrons in Iowa differed from this. The majority of mature females being found without macroscopic ova, and most males being at the peak of their reproductive capability only in early summer.

Mean number of mature ova was 2626 (range, 3844 to 1645). The only account in the literature of ova numbers that could be found was from Ball (1936). He reported a range of 800 to 2000 ova for S. holbrooki in Connecticut. The larger number of ova produced by S. bombifrons in Iowa may have contributed to the presumed rapid expansion of this species in the loess hill of the state.

Mean ova size was 1.29 mm (range, 0.71 to 1.6). A large number of unpigmented immature ova was also present in each ovary. Mean size of these ova was 0.573 (range, 0.378 to 0.903). Trowbridge (1941) reported a mean mature ova size of 1.5 mm for S. bombifrons. Zweifel (1968) reported a mean of 1.58 mm for S. bombifrons, 1.34 and 1.44 for S. couchi, and 1.6 and 1.16 for S. hammondi. No mention of immature

ova was made in these studies. It might be expected that if Iowa Scaphiopus produce more ova than elsewhere the mean size could be reduced. This is especially true when the frogs are not larger than elsewhere.

Mean adult fat body weight was 0.304 gm, and mean juvenile fat body weight was 0.037 gm. For adults fat body weight was highest in July and lowest in August (Fig. 8). The mean weight increased from May to June, indicating the accumulation of fat stores was not severely affected by breeding in June, although accumulation of fat in April and May, while ova were growing, may well have been slowed. The sharp July to August drop in fat body weight in adults was probably due to the addition to the population of newly matured individuals. The actual fat body pattern could have been masked by the appearance in the sample of newly matured juveniles and the disappearance of adults.

For juveniles fat body weights were lowest in May and highest in September (Fig. 9). The mean dropped from June to July, probably caused by the addition to the population of newly metamorphosed young. The mean then increased until September, as would be expected since fat was accumulated for hibernation. No accounts could be found in the literature where fat bodies were measured for Scaphiopus of any species, so comparisons could not be made.

SUMMARY AND CONCLUSIONS

S. bombifrons was found to occur throughout the loess hills and the adjacent flood plain, and evidence suggested it was a recent invader. At the time of this study, spade-foots were moderately abundant and the species was clearly not worthy of threatened or endangered status. Iowa now represents the northeastern extreme of the species' range in North America. The east-west range in Iowa could not be established conclusively, and substantial searches made to the east, where the loess is thinner, revealed no Scaphiopus. Further studies are needed to determine whether or not the species occurs east of the deep loess.

A partial albino adult S. bombifrons was collected in Monona County, Iowa. Further sampling would reveal the extent of albinism in the population.

More adult males than adult females were found, but the difference in sex ratio may have been due to behavioral differences between the sexes. Females seemed to disappear from the population nearly two months before males. The reasons for this behavior were not clear.

Adult females were significantly larger than males, and they appeared to reach maturity at a more consistent body size. The data were consistent with the measurements of S. bombifrons elsewhere.

S. bombifrons in Iowa appeared to have a well-marked breeding season, with most individuals breeding only once,

usually in June. Occasionally unfavorable conditions could delay breeding until later in the season. Most Scaphiopus were inactive at an air temperature of around 60°F. This was a somewhat higher minimum activity temperature than reported for Scaphiopus elsewhere.

The data suggested that most S. bombifrons juveniles in Iowa matured in time to breed in their second year, while perhaps a few slow growing individuals, or late hatchlings did not breed until their third calendar year. Age at maturity was less than reported for Scaphiopus elsewhere. Most adults appeared to persist in the population for two years, although the appearance in late spring of a few large adults implied that some persisted in the population for longer.

June was dominated by adults emerging to breed, but most adults dropped out of the sample after July, probably due either to death or aestivation. They did not re-emerge with August or September rains. Adult S. bombifrons and S. holbrooki from Oklahoma and Connecticut respectively were found to emerge independent of rain to forage in summer. Juveniles were active through September in Iowa.

Testes length and ovary weight were both greatest in June. These data tended not to support a xeric breeding pattern as described by Bragg (1945a). However, at least one individual with mature ova and one with spermatozoa were found during each month of activity, supporting the xeric

pattern to a degree.

As many as 1800 more ova were produced by S. bombifrons in Iowa than were reported for S. holbrooki in Connecticut. This may have contributed to the presumed rapid expansion of this species in the state. The mean number of ova produced in Iowa was 2626. S. bombifrons from Iowa had smaller ova than those studied elsewhere, which might be expected if they produced more ova and were not larger than spadefoots from other localities. Mark-recapture studies could add useful information concerning length of life, number of breeding periods per year, survival over winter, growth, and could enable estimation of local population.

Adult fat bodies were largest in July and smallest in August. They increased from May to June, indicating that the accumulation of fat stores was not severely affected by breeding in June. The July to August decline was probably due to the addition of newly matured individuals to the population. Juvenile fat body weights were lowest in May and highest in September, with a decline from June to July, probably caused by the addition to the population of newly metamorphosed young. They grew through September as fat was accumulated for hibernation.

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